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LOCALIZED STAGES IN COMMON ROADSIDE PLANTS.

JOSEPH A. CUSHMAN.

THE plants considered in the present study are of common occurrence along country roadsides. With, perhaps, the exception of some of the early stages of development, the leaf forms noted may be found on country roads in the spring or summer. Although among our commonest plants, some actually classed as weeds, the stages shown in their development are as striking as could be found in any plants. The stages in development of other common plants have been described (*Amer. Nat.*, Vol. 36, No. 361), as well as some exotic plants of the Botanic Gardens of Harvard University (*idem.*, Vol. 37, No. 436). My thanks are due to Dr. R. T. Jackson for corrections and helpful suggestions. Each species is treated separately and its stages described in detail.

Thalictrum polygamum Muhl. Figures 1, 2.

(Tall Meadow Rue.)

Although this plant does not become conspicuous by its flowering until midsummer, its early growth from the rootstock and seedlings must be looked for in moist ground very early in the spring.

In the seedling (Fig. 1) the first nepionic leaf is simple, with three lobes. Such a first leaf is frequently found, but fully as often the first leaf is like the second leaf in the figure. The second leaf is trifoliolate, each leaflet being like the whole of the first nepionic leaf as figured. From this point the leaves of the young plant, as added, increase in complexity, the plant finally producing the 2–3 ternately compound leaves characteristic of the adult.

As the plant is a perennial its early spring growth may be easily studied.

When first noted it usually has complicated leaves, but if the very earliest growth is looked for, leaves will be found exactly comparable to those of the seedling. The trifoliolate form is commonest, but in some cases, especially where the plants grow in sandy soil, the first leaf will be simple, as in the first leaf of the seedling. The steps in the further complication of the compound leaf follow the same stages as in the seedling, but usually more rapidly, arriving at the typical leaf of the species by fewer stages than in the seedling. This is a good example of acceleration of development seen in localized stages.

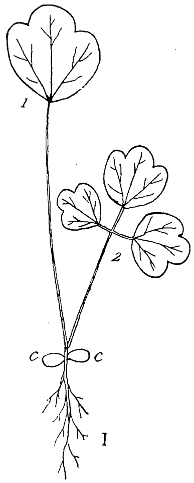


FIG. 1.—Seedling of *Thalictrum polygamum*, showing cotyledons, *c*, *c*, and first and second nepionic leaves, the first with 3, the second with 5 leaflets.

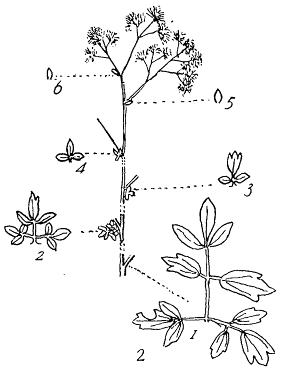


FIG. 2.—Flowering stalk of *Thalictrum polygamum*, showing localized reversionary senescence below the flower. Leaves 1-6 enlarged to natural size.

The plant produces great masses of the small flowers, and the strength thus used up is deducted from the amount which goes to leaf development, with the result that below the flower there is always shown localized senescence, exhibiting regressive development. Figure 2 shows leaves in the series below the flower panicles. There is a gradual reduction of the proximal portion as shown in leaves 1 and 2, until a leaf is produced (Leaf 3 of Fig. 2), in which the leaf is trifoliolate, as in leaf 2 of Figure 1, but having no lobes on the lateral leaflets. Next, the lobes of the terminal leaflet are reduced and the outline of all the individual leaflets thus becomes entire. Still later the two lateral leaflets disappear and a very small, simple, entire leaf is found (Leaves 5 and 6), simpler than anything seen in progressive development, either in the straight development of the seedling or the localized development in early spring growth. The stages below the flower are very noticeable and are easily made out.

Daucus carota L. Figures 3–13.

(Wild Carrot.)

In this common weed very marked localized stages are found. The direct development of the seedling shows much acceleration as the first leaf of the ordinary seedling is considerably complex. The first nepionic leaf of the seedling of this species is shown in Figure 3. It is a decidedly compound leaf. The second leaf is still more complex.

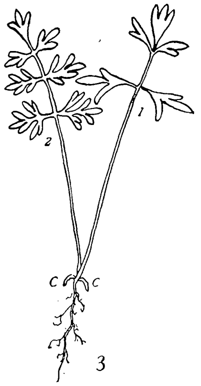
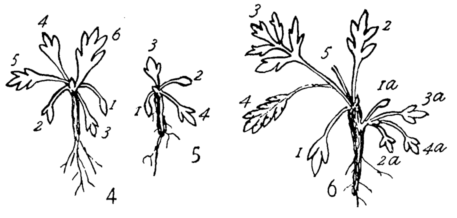


FIG. 3.—Seedling of *Daucus carota*, showing cotyledons, *c*, *c*, and first and second nepionic leaves.

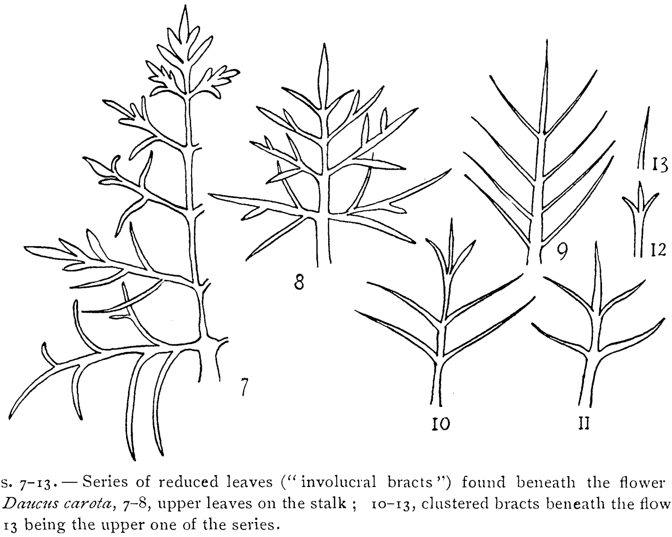
The spring growth is to some degree difficult of investigation, as the plant starts its growth very early. The first leaves seen under usual conditions of growth are very complex. It was therefore a matter of some trouble to obtain specimens showing reversionary characters. Finally plants growing under unfavorable conditions were sought. There the results were most gratifying. The plants shown in Figures 4–6 were found growing in sand along a railroad embankment where the conditions were decidedly adverse. They are of course weak specimens, although the size of the stem shows them to be adult plants of at least one year's growth.



FIGS. 4–6.—Spring growths of *Daucus carota*, 5–6 (1*a*–4*a*), weak growths; 4–6 (1–4), more vigorous growths.

In Figure 4, the first leaf of spring growth is simple and entire, the second leaf is similar but with a lobe on one side, the third leaf is trilobate and the fourth also. The fifth and sixth leaves have five lobes. In Figure 5, the stages except in the second leaf are exactly similar. From the plant shown in Figure 6 two buds started. The series from the lateral weak bud, 1*a*–4*a*, are in the main like those of Figure 5, but the series from the stronger bud, 1–4, show a greater acceleration of development. The first leaf, No. 1, is comparable to the third leaf of Figures 4 and 5 and the third leaf of weaker growth on this same plant. The second leaf, No. 2, is comparable to the fifth leaf of Figure 4, and the third leaf is more complex than anything shown in the other cases of spring growth figured, but is closely comparable to the first nepionic leaf shown in the seedling (Fig. 3). In the localized development shown in early spring growth of weak plants, therefore, stages are found which are simpler than anything found in the direct development of the seedling. In vigorous plants spring growth is so much accelerated that these simpler stages are not found.

In Figures 7–13 are shown the leaves beneath the flower. Figure 7 shows the typical adult leaf of the stem, Figure 8 the upper leaf on the stem in the specimen examined. By comparing Figure 8 with the second nepionic leaf of the seedling (Fig. 3), it will be seen that the two are very similar except that the leaf tips are more acute, almost spiniform. Below the flower cluster there are what are usually termed "cleft involucral bracts." These



FIGS. 7–13. — Series of reduced leaves ("involucral bracts") found beneath the flower of *Daucus carota*, 7–8, upper leaves on the stalk ; 10–13, clustered bracts beneath the flower, 13 being the upper one of the series.

are really reduced leaves as they are the morphological equivalent of such. Figure 10 is, in the number of its main division, comparable to the first nepionic leaf of the seedling (Fig. 3), and to leaf 3 of Figure 6 in the early spring growth. It differs however in not showing secondary lobes as seen in the other cases. Leaves of the next succeeding whorl have five main lobes, Figure 11, comparable to leaf 2 of Figure 6, or to leaf 5 of Figure 4. The one shown in Figure 12 is comparable to leaf 3 of Figure 4, or to the second stage in early spring growth. Figure 13 shows the ultimate reduction and a simple leaf comparable to the simplest first stage of spring growth. This series below the flower repeats in the reverse order, the steps shown in the progressive localized development of early spring growth and in the direct development of the seedling. In other words, it is regressive development repeating progressive development, but in the reverse order.

Baptisia tinctoria R. Br. Figures 14–16.

(Wild Indigo.)

This plant shows localized stages in a simple manner, yet very completely. In the direct development frequently starts off with the first nepionic leaf simple, broad and rotund, distally emarginate, the stipules not large but nevertheless noticeable (Fig. 14). The first leaf is broader and more rounded than the type leaf of the species (Leaf I of Fig. 16) in which the tip is slightly mucronate instead of slightly emarginate. The second nepionic leaf is trifoliolate, the leaflets rounded, wedge-obovate. The succeeding leaves are all trifoliolate, the stipules becoming smaller and less persistent.

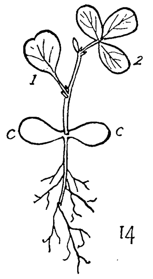


Fig. 14.—Seedling of *Baptisia tinctoria*, showing cotyledons, *c*, *c*, the first and second nepionic leaves, the first simple, the second trifoliolate.

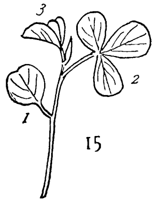


Fig. 15.–Early spring growth of *Baptisia tinctoria*, showing localized stages comparable to direct development seen in seedling.

Comparing these stages in direct development with localized stages in development seen in early spring growth, the similarity is at once apparent. In some plants, probably but a year old, there were found many cases where the first leaf of spring growth was simple and emarginate, but like that of the first nepionic, much broader than the later leaves (Fig. 15). The stipules were also larger than in succeeding stages and in this again comparable to the first nepionic leaf of the seedling, showing a more accelerated condition. In all cases the second leaf of spring growth was trifoliolate. Those which were found with the spring growth starting off with a simple leaf were obtained in a situation unfavorable to the plant and thus favoring such retarded conditions of growth. The overlying loam had been removed from a glacial sand plain, leaving the sand exposed on a south slope. This gave a poor supply of moisture and exposed the plants to the full force of the sun. As a result, the plants showed a retarded development.

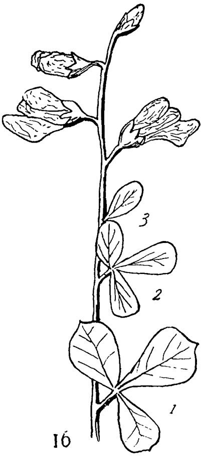


FIG 16.—Flowering stalk of *Baptisia tinctoria*, showing the reduction of characters in the localized senescence below the flower.

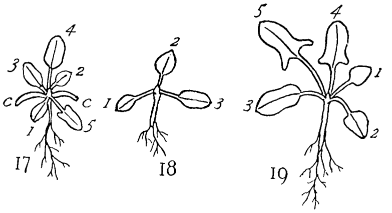
In the adult plants, when in flower, cases of localized senescence are not infrequent. Below the flowers, the last leaf is often simple, comparable to the first nepionic leaf of the seedling (Fig. 14), and to the first leaf of spring growth in feeble or retarded plants (Fig. 15). This reversionary condition below the flower is not usually shown, however.

Rumex acetosella L. Figures 17–19.

(Sheep Sorrel.)

The peculiar auricled form of the leaves of this plant furnishes a means for study of stages, although the leaf is not compound as in the preceding cases. The seedling (Fig. 17) has the first and second nepionic leaves ovate, tapering somewhat at the base and with acute apices. In the third leaf the base is broader and the tip more blunt. The fourth leaf has a much broader base and more blunt apex so that it assumes a roughly oblong shape. The fifth leaf has the auricled base characteristic of the species. Later leaves hold to this character. The early leaves of the seedling are red while later ones are green.

Turning to the early spring growth, very similar stages are noted (Fig. 18). In this weak plant the stages are exactly the same, leaf for leaf, as in the seedling after the cotyledons. In Figure 19, the early growth of a somewhat stronger plant, the first two leaves are similar to the first two of the seedling. The auricled form appears here in a vigorous plant in the fourth leaf, one stage earlier than in the seedling. The leaves in the early spring growth also resemble the seedling in their reddish color, but this is a superficial resemblance and not one of true repetition. It is dependent upon other causes.



Figs. 17–19. — Seedling and early spring growths of *Rumex acetosella*. 17, seedling, showing cotyledons *c*, *c*, and first five nepionic leaves; 18–19, early spring growths showing stages by which the auricled form of base is reached.

On the flowering stalk there is a reduction of the base in the same manner, but in the reverse order, until below the flower there are linear leaves with narrow apices and bases. Thus the first leaves of the direct development in the seedling, the first leaves in the localized development in early spring growth and the last leaves in the reversionary localized senescence below the flower are without the auricled bases. In all other parts of the plant the leaves have the auricled base typical of the species.

Potentilla canadensis L. Figures 20–23.

(Common Cinquefoil.)

In this plant the seedling usually has the first nepionic leaf simple, the second ternate (Fig. 20). Succeeding leaves are ternate but apparently five palmate, due to the splitting of the lateral leaflets into two parts as shown in leaf 4 of Figure 21, a spring growth.

The early growth of this plant from adult roots is usually strong, but some plants have simpler leaves than characterize the adult. Over a hundred young plants were examined, all in an early condition of spring growth. Of these, the great majority had already the dissected ternate leaf, typical of the plant. Between fifteen and twenty of the smaller plants had the early leaves ternate, without dissection of the lateral leaflets (Fig. 22, leaf 2). In this specimen the first two of the early leaves had this character. In only one case in the hundred or more examined was a simple leaf found as the first of the early spring growth. In this specimen (Fig. 21) the first leaf was simple, the second ternate, and the succeeding ones of the typical dissected ternate form. This shows the rarity of this stage both in seedlings and spring growth, it being usually skipped by acceleration.

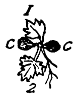


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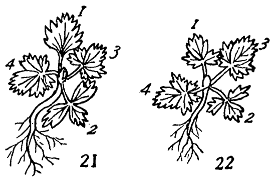
Fig. 20.—Seedling of *Potentilla canadensis*, showing cotyledons, *c*, *c*, and first and second nepionic leaves, the first simple, the second trifoliolate.



Figs. 21–22.—Early spring growths of *Potentilla canadensis*. 21, showing exceptional case where first leaf is simple.

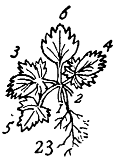


Fig. 23.—Final season's growth of *Potentilla canadensis*. A rare case in which the last leaf, no. 6, is simple, due to lack of growth force at the end of the growing season.

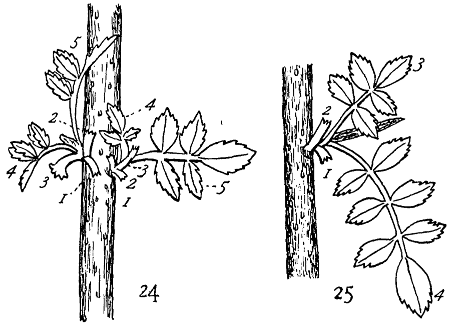
In the flowering there is usually little reduction, for the flower is comparatively very small and not confined to the end of the shoot. The leaf from the axil of which the flower comes, may be reduced to simple ternate one, but in the specimens examined no further reduction was found. In the late season's growth, however, very definite senescence is seen (Fig. 23). Plants were obtained in late November, when the leaves were nearly or quite dead, where the last leaves were reduced very frequently, to a simple ternate form, as shown in leaf 5, Figure 23. In one case out of those of this late growth which were examined, there was a simple leaf as the last leaf of the season's growth (No. 6, Fig. 23). This leaf, the last of the senescent ones of the season's growth, is comparable to the simple leaf seen in the first stage in the direct development of the seedling, and also to the first leaf of the localized development, seen in the early spring growth. This is due to the lack of strength in the latest part of the season's growth and a consequent reduction follows. In this senescence then, the same stages are found, but they are developed in the reverse order.

Sambucus canadensis L. Figures 24–25.

(Common Elder.)

This seedling of this plant was not obtained, but one of another species, *S. nigra*, is figured by Lubbock (*Seedlings*, vol. II, p. 51, Fig. 420). In this species the leaves are in pairs. The two first pairs of nepionic leaves are simple, toothed, and the third pair is trifoliolate.

In the early spring growth of our species there are first, leaf-like bracts shown in Figures 24 and 25. These are notched or toothed at the distal end. In most cases there are three of these teeth or in some cases five. These teeth seem to represent the reduced leaflets of a compound leaf — in the commonest case a trifoliolate one. In such a case the first true leaf is trifoliolate or it may have five leaflets. In some cases, after the three-toothed bract there is a five-toothed one, usually more expanded and leaflike. Such a form is not followed by a trifoliolate leaf, but, in all the cases noted, by a leaf with five leaflets. These teeth then appear to represent the reduced leaflets, for if they did not there would be no reason against producing a trifoliolate leaf directly after the five-toothed bract. These bracts might be thought of as the stage representing a simple toothed leaf, but this definite succession of a leaf with five leaflets after a bract with five teeth seems to indicate them as reduced leaflets and not true teeth.



Figs. 24–25. — Early spring growths of *Sambucus canadensis*. 24, showing the five toothed bract followed by a leaf with five leaflets.

Beneath the flower there may be a very slight reduction in the number of leaflets, but as a rule it is not carried to any noticeable extent.

Chenopodium album L. Figures 26–36.

(Lamb's-Quarters. Pigweed.)

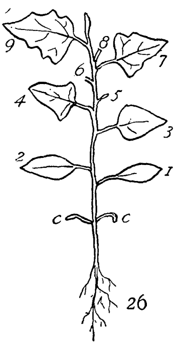
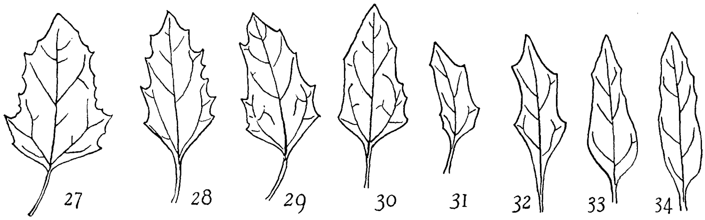
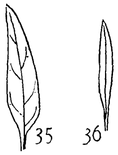


Fig. 26. — Seedling of *Chenopodium album*, showing cotyledons, *c*, *c*, and several of the nepionic leaves.

This very common weed shows excellent localized stages. It is an annual and therefore shows it simply in the localized senescence below the flower. The seedling (Fig. 26), shows the direct development. The first two nepionic leaves are narrowly oval, tapering at the base and apex, with the basal portion not broader than the similar apical portion. The third leaf has a broader base and in the fourth it has become decidedly angled. In succeeding leaves the base becomes angulate-toothed (leaf 9). This leads quickly to the adult character (Fig. 27), and is continued until flowering. Then comes the reduction shown in the series (Figs. 27–36). This series represents leaves in the axils of which branches or flowers are produced. The typical many toothed condition shown in Figure 27, is, in succeeding leaves, reduced until finally the simple leaves shown in Figures 35 and 36 are produced below the flower. The





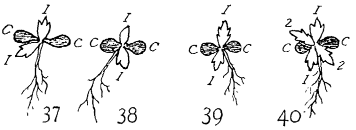
Figs. 27–36. — Series of leaves on the stalk of *Chenopodium album*, showing the stages in the reduction from 27, the typical species leaf, to 36 the linear, reduced leaf below the flower.

stages passed through are very similar to those in the direct development of the seedling, but are in the reversed order of sequence.

Achillea millefolium L. Figures 37–42.

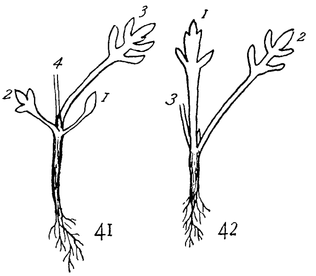
(Common Yarrow.)

The seedlings of this plant are very similar to those of *Tanacetum vulgare* L., as may be seen by a comparison of the figures of the seedlings of that plant (*Amer. Nat.*, vol. XXXVI, p. 881, Nov. 1902) with those of Achillea given here (Figs. 37–40). Both plants belong to the same tribe of the Compositæ.



Figs. 37-40. — Seedlings of *Achillea millefolium*, showing differential acceleration in different individuals. 37 and 40 showing normal individuals, 38 a retarded, 39 one that is especially progressive.

There is much variation in the seedlings as was also noted in Tanacetum (*loc. cit.* p. 871). The first pair of nepionic leaves are usually three toothed; the second pair five toothed (Fig. 40). As shown by the figures this may be decidedly varied. Figure 37 shows the typical first pair of leaves; Figure 40 in addition the typical second pair. Figure 38 shows a retarded individual where the character of a three-toothed leaf, usually taken on in the first pair of nepionic leaves has not appeared, except as indicated by a single tooth of one leaf. Figure 39 shows an accelerated individual where the character of a five-toothed leaf, characteristic of the second pair of leaves, is shoved back and appears in one leaf of the first pair.



Figs. 41-42 — Early spring growths of *Achillea millefolium*, showing differential acceleration in the localized development of two individuals, though both are more retarded than those usually found.

In the early spring growth better results were obtained than in the case of Tanacetum. Specimens of Achillea were found growing in the sandy railroad embankment which has been previously referred to. As in Tanacetum, the simplest leaves as a rule seem to be five toothed as in Figure

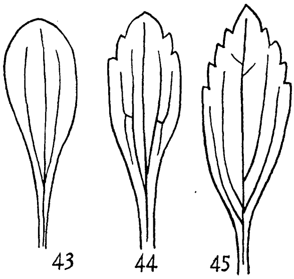
42. In rare cases, however, plants were found which had the first leaf with three teeth. In the specimen (Fig. 41), the first leaf was simple like one of the first nepionic leaves shown in Figure 38; the second was three toothed like the first nepionic leaves of the typical seedling (Figs. 37 and 40), and the third leaf has five teeth as was so commonly found as the first stage from rootstocks in the early spring growth. This then is a very retarded individual and repeats in its localized development, all the main stages seen in the whole series of seedlings representing the direct development.

Beneath the flower reduced leaves are also found. At the junctions of the stems of the compound corymb, leaves are found which are like those of the early spring growth and seedling in that they are simple and but few toothed. At the upper portion near the ultimate branchings are found leaves with five and three teeth and in some cases, simple entire leaves. These leaves are seen to repeat the same stages as in the localized development shown in spring growth and in the direct development of the seedling but in the reverse order. It is still another case of the localized reversionary senescence already referred to.

Aster acuminatus Michx. Figures 43–48.

(White Wood-aster.)

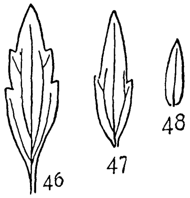
The seedling of this species was not obtained but a comparison of the early spring growth of an adult plant with the portion below the flower heads shows striking similarities. The stages are very simple, varying mainly in the number of the lateral teeth.



Figs. 43–45.— Leaves of *Aster acuminatus*, showing three of the stages from the entire radical leaf 43, to the typical species leaf, 45.

In the early spring growth of a plant a year or more old, the radical leaves are at first entire and somewhat spathulate (Fig. 43). The next leaves have two lateral teeth and succeeding leaves have two lateral pairs (Fig. 44). In further development three lateral pairs are produced and in the mature condition the leaves have four pairs, as in Fig. 45, which represents the typical leaf of the species.

Leaves like that shown in Fig. 45 are produced until the time of flowering. Then a reduction in the number of teeth takes place. Leaves with four, then three, pairs of lateral teeth are produced and nearer the flower heads, leaves with two pairs are shown in Fig. 46, later with the single pair (Fig. 47), and finally below the flower, the simple leaf shown in Figure 48. The reduction here is carried on in a definite manner and retraces exactly, in reversed order, the same stages that are passed through in the early spring growth, so that, using numbers for the lateral teeth, we may represent the stages graphically, calling the entire leaf number 1, as follows:



Figs. 46–48. — The three final stages in the localized senescence below the flower of *Aster acuminatus*, 48 showing the last stage in the reduction.

Early spring growth to Flowering
1, 3, 5, 7, 9 . . . . . . 9, 7, 5, 3, 1.

Eupatorium perfoliatum L.

(Thoroughwort. Boneset.)

This well known plant shows in its leaf characters certain things which may be noted here as in the same line with the preceding cases. The main leaf character of this plant is the connate-perfoliate form of the leaf. This, however, by an examination of a flowering specimen, will be seen to occur on only a part of the stem. In the early spring growth of the plant, the bases of the opposite leaves are free and narrow. Later the coalescent form is taken on and kept until well toward the flowering. Then the early form is again taken on, the base of the leaves being narrowed and failing to meet.

A variety of this species, var. *cuneatum* Engel., is apparently a more primitive form. It keeps the early character throughout its life history, the leaves failing to coalesce at their bases. This variety also has fewer flowered heads than the typical form of the species.

The commonest plants illustrate well the principle of localized stages in development seen in the direct progressive development of the seedling, in localized stages of spring growth and in the localized senescence at flowering. It may be shown in a variety of ways, as noted in the present paper. In Thalictrum, Baptisia, etc., it was shown especially by change in the number of leaflets; in Rumex, by the changes in the auricled base; in Daucus, etc., by the change in the number of the teeth, and finally in Eupatorium, by the presence or absence of the connate form of the leaf.

Different individuals show variations due to differences in acceleration of development. There is a differential acceleration in individual seedlings, shown where the first nepionic leaf in various individuals is more progressive or more retarded than in the typical cases. In spring growth it is also shown in much the same way, and with a still wider range of variation. These differences in acceleration may be caused by poor conditions, such as poor soil, lack of sufficient moisture, cold, etc., and by internal causes not accounted for in the above.

Regressive development, seen in the localized senescence below the flower, is shown in many cases to be more reversionary than stages in the usual seedling. When a large number of seedlings are examined, however, such extreme cases of variation may be seen which would otherwise be overlooked.

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